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ANTITHETIC *VERSUS* HOMOLOGOUS ALTERNATION.¹

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THE nature of the alternation of generations in Archegoniates is a question of fundamental importance in dealing with the morphology of the vascular plants, and necessarily has been the subject of much discussion, with a corresponding divergence of opinion. Both the antithetic and homologous nature of the alternation of generations have been supported by such eminent advocates that one hesitates to speak too confidently on either side. As I cannot, however, after long and careful study, agree that the argument is equally strong for both sides, and it seems to me that proper weight has not always been given to some of the evidence, it has seemed worth while to review the direct evidence on both sides as completely and as fairly as possible.

I shall not enter into a detailed account of the controversy, as that has already been done quite recently.² I have myself given fully my own reasons for supporting the antithetic theory.³

¹ Read before Section G. at the Washington meeting of the A. A. A. S.

² Coulter: The Origin of the Leafy Sporophyte. *Bot. Gaz.* July, 1899.

³ Campbell: *Mosses and Ferns*, pp. 510-514, 1895.

and it seems to me that Professor Bower¹ has effectually refuted the arguments of Dr. Scott, who has been the special champion of the homologous theory in England. More recently Mr. W. H. Lang has reviewed the subject,² being more or less non-committal, but rather leaning to the homologous view; and in this country Professor Coulter³ has assumed a somewhat similar attitude.

Owing to their perishable nature, the simpler green Algæ and Bryophytes have left very meagre fossil remains, so that their geological history is very imperfect, and we are perforce driven to a study of the living forms, as practically our only means of tracing the ancestry of the higher plant forms. Of the vascular plants there are abundant fossil remains which throw much light upon the relationship of the Pteridophytes and seed-plants, and the succession of forms in geologic times, but help but little in determining the lower forms from which the former originated.

It has been urged that inasmuch as ferns, and even seed-plants, can be traced back to the Devonian, and possibly even further, it is hopeless to expect the secret of the origin of the vascular plants can ever be solved. However, as many extremely primitive forms have undoubtedly survived to the present time, we can learn very much from a comparative study of these with the higher plants, which must have come from forms very similar to them. Of the forms which are of special importance in this connection are the simpler green Algæ, and the generalized liverworts.

Zoölogists are in much the same position with regard to the origin of the vertebrates, as botanists are concerning the vascular plants. The former sub-kingdom is certainly as old and probably older than any land-plants—and yet we do not find that the zoölogists consider the question of the origin of vertebrates entirely hopeless.

I shall not attempt here to discuss the monophyletic or polyphyletic origin of Pteridophytes, but shall mainly concern myself with the class which at present is the predominant one, the Ferns.

¹*Nature*, Nov. 17, Nov. 24, Dec. 1, 1898.

²*Annals of Botany*, 12: 585-592, 1898.

³*loc. cit.*

According to the antithetic theory of alteration, the ferns have originated from forms very similar to the simpler existing liverworts, the leafy sporophyte being an elaboration of the non-sexual sporophyte. The homologous theory maintains that Bryophytes and Pteridophytes have nothing to do with each other, the latter arising quite independently from algal ancestors. The latter hypothesis was first suggested by the alga-like protonema of the mosses, and the somewhat similar prothallia of certain ferns, especially *Trichomanes*.

Opposed to this assumption is the fact that the filamentous prothallia of such ferns as *Trichomanes*, or *Schizaea pusilla*, are obviously secondary developments, in the former case, at least, associated with excessive moisture. The prothallia of most ferns grown in water, or kept excessively wet, and poorly lighted, tend to assume a filamentous form. Among both Hymenophyllaceæ and Schizæaceæ, the great majority of forms studied possess the normal flattened prothallium of the ordinary ferns. The filamentous protonema of the true mosses is also, if we are to trust the evidence of comparative morphology, a secondary development from the liverwort-like thallose protonema of forms like *Sphagnum*. The true mosses and Hymenophyllaceæ are probably very far from being primitive types.

From a comparison of the fossil and living ferns it is certain that the so-called eusporangiate types are much older than the leptosporangiate forms which are now predominant. The Marattiaceæ, of which only a small number of tropical species survive, are especially well represented in the Palæozoic rocks. Now on the assumption that the gametophyte of the ferns is descended directly from algal ancestors, and is not of bryophytic origin, we should expect the gametophyte of these primitive ferns to be more alga-like than that of the more recent and specialized Leptosporangiates. The gametophyte of the existing Marattiaceæ which is well known, is a fleshy, relatively large and long-lived thallus, closely resembling that of the lower liverworts, being much more like these, both as regards the vegetative growth of the thallus and the reproductive organs, than are the prothallia of the common ferns.

The gametophyte of the Ophioglossaceæ, the second order of

the Eusporangiatæ, is also very massive, and as far as possible from any known algal form. Of course in the Ophioglossaceæ, the saprophytic nature of the gametophyte has doubtless to some extent modified its structure.

The archegonia of the Marattiaceæ are extraordinarily like those of the Anthocerotaceæ, and the antheridia also offer certain suggestions of a similar origin to those of the latter order. Indeed, were it not for the biciliate spermatozoids of the Anthocerotaceæ, and their peculiar chromatophores, I should not hesitate to assume a direct connection between the latter order and the eusporangiate ferns.

The extraordinary uniformity in both structure and development of the archegonium throughout both Bryophytes and Pteridophytes, including such a marked character as the ventral canal-cell; the great similarity in the origin and development of the spermatozoids, and the details of fertilization, certainly are very strong arguments for a common origin for all Archegoniates. The theory that these resemblances are merely parallel developments can only be accepted on the production of very much weightier evidence than has yet been brought forward.

When to the obvious resemblances existing between the gametophytes of the ferns and liverworts (of course the lower types like the anacrogynous Jungermanniales and the Anthocerotaceæ being understood) there are added the numerous resemblances in the development of the sporophyte, the probability of a genetic connection between the two phyla of the Archegoniates becomes enormously greater. The fallacy of Dr. Scott's argument, that the assumption of the antithetic theory involves the creation of a structure *de novo*, without any apparent ancestry, has been perfectly refuted by Professor Bower. There is no claim that the sporophyte is an entirely new structure. It starts with the zygote, which on germination produces a greater or smaller number of spores, thus increasing the number of plants resulting from a single zygote, an obvious advantage. The rudimentary sporophyte of Coleochaete, which there is no difficulty in homologizing with the zygote-product of *Œdogonium*, may equally well be compared with the sporophyte of *Riccia*, as has often been done, whether we assume that the sporophytes of the two are genetically related or not.

As yet we have no evidence beyond mere hypothesis as to the way in which the motile zoöspores, arising from the zygote of the algal ancestors of the Bryophytes, gradually were replaced by the tetrads of non-motile spores which characterize all Archegoniates. The same difficulty is met with in tracing the origin of the sexual organs. In both respects there is much greater difference between the humblest liverwort and the highest alga than there is between the former and the most highly organized fern. It must be confessed that the gap between all existing Algæ and Archegoniates is very great.

When we compare the two series of Archegoniates, the case is very different. The structure of the archegonium and spores is identical throughout, and the early stages of the sporophyte agree very closely, this being especially true of the more primitive types of Pteridophytes. In these the young sporophyte remains very much longer dependent upon the gametophyte and the external organs which characterize the Pteridophytes, are relatively late in making their appearance. Both of these facts point to a nearer approach to the bryophytic type in the lower Pteridophytes, a fact which is not readily explicable on the assumption that they are in no way connected with the Bryophytes. In a number of the lower Pteridophytes, *e. g.*, *Marattia* *Lycopodium*, *Botrychium*, the young sporophyte may remain attached to the gametophyte for months, or even years, long after it has passed beyond the embryonic stage.

If we compare the gametophyte and sporophyte of any typical Archegoniate, we note a very significant difference in their relation to the water-supply. The gametophyte is always, to a greater or less degree, an aquatic organism, never quite emancipating itself from the life conditions of its algal ancestors. The sporophyte, on the contrary, at least in its earlier stages, is never exposed directly to the water, although a few groups of Pteridophytes have developed, secondarily, aquatic sporophytes. Almost from the first the sporophyte is provided with a special massive absorbent organ, the foot, which is later superseded by the true roots of the Pteridophytes, a much more efficient means of obtaining water than is provided by the rhizoids of the gametophyte; and the unlimited capacity for growth of

the true roots of the vascular plants allows the development of a root system to keep pace with the growth of the aerial part of the sporophyte. There is thus developed for the first time a plant-body strictly terrestrial in its character, and capable of independent growth.

The gradual elaboration of the sporophyte is easily traced in the liverworts from the simple capsule of *Riccia* to the large and almost independent sporophyte of *Anthoceros*, or in another direction to the elaborate sporophyte of the true mosses.

Whether or not we agree entirely with Professor Bower's beautifully worked out theory of the sterilization of potential sporogenous tissue, the fact is patent that there has been a gradual elaboration of the originally purely sporogenous and parasitic structure resulting from the zygote, in the direction of an independent plant, with a corresponding subordination of the spore-producing function to the vegetative life of the sporophyte. This culminates among the Bryophytes in such highly specialized types as *Polytrichum* and other similar mosses. In these there is early developed a foot, which supplies the materials needed for the growth of the long-lived sporophyte. In the more highly organized forms there is present a special strand of water-conducting tissue, which may be directly compared to the fibro-vascular bundles of the higher plants. The outer tissues of the long slender seta, also, assume the character of mechanical tissues which give it the necessary strength to support the large and complicated capsule, in which only a very small amount of tissue is devoted to spore-formation.

At an early period the outer tissues of the sporophyte develop chlorophyll, and there may be formed a distinct assimilative organ, the apophysis, provided with green lacunar tissue communicating with the external atmosphere by means of stomata, entirely similar to those upon the green organs of the vascular plants. The highly specialized sporophyte of the true mosses has not probably given rise to any type of vascular plants, but in the equally developed, but much more generalized sporophyte of *Anthoceros*, we have a structure that may well represent the characters of the sporophyte from which originated the leafy sporophyte of the ferns.

Perhaps the strongest argument in favor of a common origin for the sporophyte in all Archegoniates is the absolutely uniform method of spore production. However ignorant we may be of the transition from the motile zoospores resulting from the germinating zygote of the green Algæ to the immobile tetrad-spores of the Archegoniates, there is no question as to the practical identity of the spores, both as to origin and structure throughout not only the Archegoniates, but the seed-plants as well. This extraordinary uniformity is perfectly comprehensible if we accept the antithetic view, since the beginning of the sporophyte must have been a simple mass of such spore-tetrads; and in *Riccia* we still have a sporophyte which has scarcely advanced beyond this stage. In the more highly developed sporophytes of the higher Archegoniates, the spores have retained their primitive characters, but a continually increasing amount of the sporophytic tissue has been devoted to purely vegetative purposes. That this formation of spore-tetrads should invariably have taken place in structures which are *secondarily* spore-producing, as is demanded by the theory of a non-sexual origin for the sporophyte in the Pteridophytes, requires something more than mere hypothesis to give it much credence. This is all the more the case if a polyphyletic origin for the different phyla of Pteridophytes is assumed.

Of all existing Bryophytes there is no question that *Anthoceros* offers the nearest approach to the Pteridophytes, although this by no means implies that the latter are directly derived from the former. Were it not, however, for the form of the chromatophores and spermatozoids in the *Anthocerotaceæ* I should not hesitate to assume this to be the case.

The sporophyte of *Anthoceros* is characterized by a long-continued basal growth that adds to the tissues of the sporophyte, which thus may reach a length of several centimeters. The origin of the sporogenous tissue is like that of the Pteridophytes, arising from sub-epidermal tissue, differing from all other Bryophytes except *Sphagnum* in this respect. Moreover the sporogenous tissue is not continuous, but is more or less regularly divided into sporogenous areas by intervening sterile tissue suggesting an approach to a very simple form of sporangium. The

highly developed chlorophyll-tissues, and the central strand of conducting tissue, apparently the true homologue of the primary vascular bundles of the Pteridophyte embryo, are certainly suggestions, if not forerunners, of the corresponding pteridophytic structures. To my mind there is far less difference between the sporophyte of such a simple Pteridophyte as *Ophioglossum* or *Phylloglossum* and that of *Anthoceros*, than there is between the latter and *Riccia*.

When Professor Coulter, for example, says, "In contrasting the sporophytes of Bryophytes and Pteridophytes, they seem to have nothing in common except that they are usually derived from the oospore and represent an asexual generation," we feel that the question has not been fairly stated. As we have tried to show, the sporophytes of the higher Bryophytes and Pteridophytes agree closely in the following important particulars: The early divisions of the embryo; the development of a special absorbent organ, the foot, thus inaugurating the terrestrial habit of the sporophyte; the gradual subordination of the spore-function, and even an approach to the formation of sporangia in *Anthoceros*; the development of special chlorophyll tissue and in some cases of an assimilative organ, the apophysis; the development of special conducting tissue; and finally the absolute identity in the character and formation of the spores, with the characteristic reduction in the number of chromosomes. These may be all mere parallel developments, and not genuine homologies; but it will require a great deal of direct testimony to make this in the least degree probable, especially when to these obvious resemblances in the sporophyte are added the equally remarkable correspondences in the structure of the gametophyte of the liverworts and ferns.

Again, when Professor Coulter says that the sporophyte of the Bryophytes never develops lateral members, and has nothing comparable to sporangia, his statement is open to question. While the complicated apophysis of a *Polytrichum* or *Splachnum* may not be strictly an appendicular organ, it may assume a flattened, leaf-like form in *S. luteum*, comparable to a perfoliate leaf, and is as truly a photosynthetic organ at least in its younger condition, as is the leaf of a fern. Of course I do not mean to

intimate that the apophysis of *Splachnum* is genetically related to the leaves of the Pteridophytes; but it is no more associated with spore-production than they are, and shows the capacity of the sporangium of the Bryophyte to produce special vegetative organs in no way connected with spore-production. The segregation of the spore-masses, already spoken of in connection with *Anthoceros*, is at any rate a hint of the origin of the sporangia of the Pteridophytes. As to the overwhelming tendency to spore-production in Bryophytes, while this is undoubtedly true of the simpler types, it may well be questioned whether it can properly be asserted of the most highly developed ones. It would be an interesting problem, for instance, to compare the relative output of spores in *Polytrichum* and *Osmunda cinnamomea*.

While it is inconceivable that such an extremely specialized structure as the sporophyte of the higher Mosses could have given rise to the leafy sporophyte of the Pteridophytes, it is quite conceivable that both types may have originated from a common ancestral form, which may very well have been not very different from *Anthoceros*. That the latter is "hopelessly specialized" is very far from being the case. On the contrary, the sporophyte of *Anthoceros* is a remarkably generalized structure. I mean by this, that it has not a single character which is peculiar and cannot be duplicated elsewhere.

Pringsheim, the first advocate, I think, of the homologous theory of alteration, based his conclusions upon the behavior of various mosses in which the protonemal filaments may arise directly from the sporophyte. Pringsheim believed that the protonema was not essentially different from the vegetative tissues of the sporophyte, from which they arose in such cases. This reasoning is not entirely convincing. The protonema arises normally from special sporophytic cells, the spores, and it is difficult to see why, under abnormal conditions, it might not arise from other sporophytic tissue. The same reasoning will apply to apospory in the ferns where the gametophyte may arise directly from the leaf-tissue.

The strongest argument in favor of homologous alternation is the occurrence of apogamy, or the origin of the sporophyte as a vegetative bud from the gametophyte. So far as I am aware

(I make this statement with some reserve) all cases of apogamy yet observed have been in cultivated ferns. At any rate, much the larger number of observed cases have been under artificial conditions, either intentional or otherwise. This suggests at once that apogamy is a pathological phenomenon. In most cases it is induced by preventing fertilization, which would otherwise take place, except in a very small number of instances. Exposure to strong sunlight has also been found to be a factor in inducing apogamy. It is also noteworthy that most cases of apogamy occur in varieties which differ from the normal in being crested, or that show other indications of exuberant vegetative growth which may certainly imply some connection between this redundant growth and apogamy in the gametophyte.

Finally, as Professor Bower has pointed out, all cases of apogamy recorded occur in leptosporangiate ferns, admittedly the most recent and most specialized members of the class. No Bryophytes nor eusporangiate ferns have yet been found which exhibit apogamy. If we are to consider apogamy as in any sense a reversion to a primitive condition, it is hard to see why it should be confined to these highly specialized modern types, and be entirely absent from the presumably much older and more primitive ones.

Mr. Lang¹ has given a very clear account of what he thinks may have been the course of development of the sporophyte, according to the homologous theory. He assumes that the primitive form of the gametophyte was a flattened thallus, presumably much like the existing liverworts, although he does not make this comparison. He supposes that this thallus under stress of circumstances, owing to an insufficient water-supply, may have given rise to spores, the spore-stage following the sexual stage, but being an integral part of the gametophyte, and not produced from the egg. It is assumed that in connection with this special spore-producing function, the leafy sporophyte gradually assumed its definite form, and later, but this point is not quite clear, became replaced by the similar structure arising from the zygote. Why the spores produced by this asexually produced structure should be identical with those developed by

¹loc. cit.

the non-homologous, sexually developed sporophyte of the Bryophyte, is not explained.

Mr. Lang's hypothesis does not claim to be based upon any experimental evidence, and it may be of interest to see whether there is any actual evidence bearing upon the natural behavior of the gametophyte when exposed to conditions similar to those assumed by this hypothesis.

There are many Bryophytes which are regularly subjected to complete drying up, and I should like to call attention to their behavior. Most leafy liverworts and mosses which grow upon the trunks of trees, or upon exposed rocks, simply dry up completely, and revive promptly so soon as water is furnished them, behaving thus very much as many algae do. In California, and probably the same is true of other similar semi-arid regions, nearly all of the terrestrial liverworts are perennial, and pass through the long, dry summer unharmed. This is well illustrated by several common species of middle California, such as *Fimbriaria californica*, *Targionia hypophylla*, *Fossombronina longiseta*, various species of *Riccia*, etc. In all of these species the apex of the shoot remains alive, being usually more or less perfectly protected by overlapping scales or hairs. As soon as the first autumn rains fall, the plants at once resume growth, and in a surprisingly short time develop their reproductive organs. Indeed it is quite possible that the young organs are sometimes already formed at the time the thallus ceases its growth in the spring.

In mosses it is not uncommon to find bulbils developed, these being merely arrested vegetative shoots, developed from the protonema, or rhizoids.

Among various liverworts, there have been found tubers of a somewhat different nature, and it is likely that when the thallose forms of semi-arid regions are further studied, these will be found to be commoner than has been supposed to be the case. In the case of the peculiar genus *Geothallus* of Southern California, the growing point of the thallus, with the tissue adjacent, becomes transformed into a tuber, with a large amount of reserve food developed in the central tissues. This tuber, which is buried in the earth, remains dormant through the summer, but germinates promptly when supplied with water.

In none of the species studied is there the slightest tendency shown to develop anything resembling the spores borne upon the sporophyte. It is true that some leafy liverworts develop single-celled gemmæ from the leaf-margins, and multicellular gemmæ are formed in various species; but these are not in any way associated with lack of water, nor are they in the least like true spores.

It is interesting to find that the gametophyte of some ferns has also developed the power of resisting drought. In California it is not uncommon to find large prothallia of *Gymnogramme triangularis* which have survived the summer, and the sporophyte of this fern, as well as that of various xerophilous species of Selaginella, can absorb water through the leaves, very much as is done by the leaves of mosses and liverworts. Goebel¹ has called attention to the behavior of *G. leptophylla*, where the gametophyte is perennial, and may develop tubers much like those found in the thallose liverworts. In this species the sporophyte is annual.

The point which I wish to emphasize is this: that whereas there are many cases where the gametophyte is subjected to the conditions which according to Mr. Lang's hypothesis should induce spore-formation, in no cases observed has this been the result, but the devices for surviving drought have been of a very different nature.

Dr. Coulter² thinks that the determining factor in the development of the leafy sporophyte has been photosynthesis or "chlorophyll-work." He sees no reason why such a structure as the leafy sporophyte may not have arisen non-sexually in response to the need for chlorophyll activity, and quite apart from the production of any form of reproductive bodies.

In support of this view he instances the development of the gametophoric branches in *Marchantia*, and the leafy gametophoric shoots of the true mosses. It is hardly likely that Dr. Coulter would derive the latter from the former, although such might possibly be inferred from his statement. The accuracy of his statement that "the erect structure laid hold of the game-

¹ *Outlines*, p. 200.

² *loc. cit.*

tophore, rather than the sporophyte," may be questioned. With comparatively few exceptions, the sporophyte of the Bryophytes is erect, while the shoots bearing the sexual organs, especially among the liverworts, are very often prostrate. Moreover there is in most of the latter class no development of distinct gametophoric shoots in the sense that such occur in the more specialized Marchantiaceæ and mosses. The transition from strictly thallose forms like *Aneura* or *Pallavicinia* to genuine leafy forms like the typical *Acrogynæ* is extremely gradual, the leafy shoots of the latter forms being in no sense buds from a thallose gametophyte, but direct transformations of the whole body of the latter. We are, therefore, perfectly justified in homologizing the leafy moss plant including of course the protonema, with a thallose liverwort or with the prothallium of a fern.

Dr. Coulter thinks that the spores would find more favorable conditions upon a leafy shoot than upon a thallus, which is doubtless true; but why this leafy shoot should not develop gradually from the sexually-produced sporophyte of the Bryophytes, as there is the strongest evidence that it has done, he does not make clear. The development upon the leaves, of spores of the same type as those of the lower Archegoniates, is entirely comprehensible, if we assume that the leafy sporophyte of the ferns is descended from a leafless bryophytic sporophyte; but it is hard to understand if we assume that the spores of the ferns have no genetic connection with the absolutely similar ones of the Bryophytes.

According to Dr. Coulter's hypothesis, the leafy sporophyte originates as a vegetative shoot from the gametophyte in a manner analogous to the production of the gametophoric shoots in the mosses, or the apogamous origin of the sporophyte in some ferns. Upon the leaves, which originally were purely organs for photosynthesis, were developed secondarily the sporangia. The germination of the non-sexual spores and of the zygote are assumed to have been entirely similar, giving rise first to a thallus, from which secondarily the spore-bearing leafy shoot arose. If such has been the course of development, it is strange that all trace of the thallose portion has been lost in the sexually produced sporophyte. One would expect to find some trace of

it in the embryo, at least of the lower types, but nothing which can be so interpreted is ever found, unless we might consider the suspensor of the Lycopods as of this nature, which probably no morphologist would be likely to do.

The statement that it is no more difficult to imagine the gametophyte producing spores, than the spore giving rise to the gametophyte, can hardly be admitted. The spores of all Archegoniates, if we assume the antithetic theory of alternation, are the direct descendants of those produced by the germinating zygote in the ancestral forms, which on germination give rise to the gametophyte. This is perfectly demonstrable, while anything like the production of spores, at least of the type produced by the sporophyte, is absolutely unknown in any gametophytic structure. The supposed cases of the production of sporangia upon the gametophyte have been shown to be merely a greatly reduced case of apogamy.

Of course, if we should admit that the sporophyte originated apogamously in the first place, it would follow that foliage leaves are older than sporophylls, and that Pteridophytes and Bryophytes have nothing to do with each other; but the weight of evidence is very much against such a supposition.

That chlorophyll-work has been a very potent factor in the evolution of the plant-body is of course beyond dispute; but its bearing upon the origin of terrestrial plants is not so clear. All green plants, whether aquatic or terrestrial, must make provision for photosynthesis, and we find the arrangements for the most favorable display of green tissue developed in various ways. Leaves are by no means confined to land-plants, many Algæ, especially the larger Phæophyceæ, having foliar organs which, although simple in structure, are often of great size, and efficient organs for photosynthesis. There is abundant evidence, also, that leaves have been developed more than once among the mosses and liverworts.

It is rather an exaggeration to say that the greater part of the chlorophyll-work in any liverworts is relegated to the gametophoric branches. Surely the amount of chlorophyllous tissue in the thallus of all the Marchantiaceæ is greater than that in the gametophores. It may also be questioned, moreover, whether

the elevation of the receptacles, which usually does not begin until after the fertilization of the archegonium, is not more intimately associated with spore-dispersal than with the need of chlorophyll-work. In most Marchantiaceæ the seta is very little developed, and the elongated stalk of the receptacles probably takes its place.

If one were looking for gametophytic structures which most nearly simulated the organs of the leafy sporophyte it would be among the lower thallose Jungermanniales, and not among the true mosses, that one should look. The extraordinarily fern-like aspect of certain thallose liverworts like certain species of *Aneura* and *Hymenophyllum*¹ recalls at once some of the Hymenophyllaceæ with fan-shaped, dichotomously veined leaves. These fern-like liverworts develop a rhizome-like stem, having flattened, dichotomously branched green shoots, curiously like a small fern leaf. Structurally, however, they are in all respects like the prostrate thallus of other species.

Now it is conceivable that when the sporophyte reached the stage when it first developed a leaf, the latter should tend to assume a form suggesting the expanded, dichotomously branched lamina, so characteristic of nearly all the lower liverworts, which I assume represent the ancestral type, from which the ferns have been derived.²

When Professor Coulter speaks of the subordination of chlorophyll-work to spore-formation among the Bryophytes, I suppose he is referring to the sporophyte. The rarity of sexual organs, and consequently of the sporophyte with its spores, is a familiar phenomenon in many mosses and liverworts. Thus whole *Sphagnum* swamps without a sporophyte, and *Lunularia* multiplying almost exclusively by vegetative buds, illustrate this. It cannot, therefore, be that lack of vegetative energy has prevented the Bryophytes from becoming predominant terrestrial forms. It is perfectly clear that purely vegetative shoots may be produced; but that these ever gave rise to the leafy sporophyte is quite another question.

The suggestion³ that the archegonium may have been derived

¹ Goebel, *Organographie der Pflanzen*, second part, p. 251.

² Campbell, loc. cit., p. 509.

³ Coulter, loc. cit., p. 58.

from a group of oögonia, protected by sterile tissue, is a novel one, but it is hard to see upon what evidence it is based. Of the algal forms, the structure of the oögonium of the Characeæ resembles most nearly that of the archegonium; but that this is anything more than an analogy is questionable, and at present it must be confessed that the origin of the archegonium is extremely obscure.

As to the significance of apospory and apogamy, both of these phenomena may, I think, fairly be compared to the various types of adventitious budding. We know that among both ferns and seed-plants, adventitious shoots may arise from almost any portion of the plant-body. The whole sporophyte may develop as an adventitious bud upon the root, leaf, stem, or even from the sporangium, shown by the budding of the nucellus in several cases of polyembryony, or the replacing of the sporangium by a shoot in *Isoetes*. Surely no morphologist would claim that because in *Camptosorus* or *Cystopteris* the sporophyte may arise as a bud upon the leaf; or in *Populus* or *Ailanthus* may spring as a bud from the root; that these facts indicate that such was the original origin of the sporophyte, and that the latter is directly homologous with the organ from which it arises.

I think, therefore, that we must fall back upon the question of water-supply as the real explanation of the peculiarities of the leafy sporophyte. All mosses remain to a certain extent aquatic, most of them absorbing water at all points much as an alga does, and depending only to a limited degree upon the rhizoids as a means of water absorption. Moreover the rhizoids are entirely inadequate to supply a plant body of large size, which could not, of course, absorb sufficient water for its needs from the atmosphere. Nature has, apparently, made numerous attempts to adapt the essentially aquatic gametophyte to a terrestrial environment, with very imperfect success.

The sporophyte, at first a purely spore-producing structure, has been from the beginning essentially aerial in habit, never being directly in contact with water, but getting its water-supply indirectly, at first through the cells of the gametophyte, but soon developing a special massive absorbent organ, the foot, the

forerunner of the root developed later, which puts the sporophyte into direct communication with the earth, thus rendering it independent of the gametophyte. With the establishment of a true root-system, capable of unlimited development to keep pace with the growth of the aerial portions of the sporophyte, there began a new era in the history of the vegetable kingdom, which has culminated in the myriad types of vascular plants which now cover the earth.